

Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches

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Abstract: Ecologists and foresters have long noted a link between tree growth rate and mortality, and recent work suggests that interspecific differences in low growth tolerance is a key force shaping forest structure. Little information is available, however, on the growth–mortality relationship for most species. We present three methods for estimating growth–mortality functions from readily obtainable field data. All use annual mortality rates and the recent growth rates of living and dead individuals. Annual mortality rates are estimated using both survival analysis and a Bayesian approach. Growth rates are obtained from increment cores. Growth–mortality functions are fitted using two parametric approaches and a nonparametric approach. The three methods are compared using bootstrapped confidence intervals and likelihood ratio tests. For two example species, *Acer rubrum* L. and *Cornus florida* L., growth–mortality functions indicate a substantial difference in the two species' abilities to withstand slow growth. Both survival analysis and Bayesian estimates of mortality rates lead to similar growth–mortality functions, with the Bayesian approach providing a means to overcome the absence of long-term census data. In fitting growth–mortality functions, the nonparametric approach reveals that inflexibility in parametric methods can lead to errors in estimating mortality risk at low growth. We thus suggest that nonparametric fits be used as a tool for assessing parametric models.

Résumé : Les écologistes et les forestiers ont depuis longtemps noté le lien entre le taux de croissance et la mortalité des arbres. En outre, des travaux récents suggèrent que la structure de la forêt serait déterminée principalement par les différences interspécifiques dans la capacité de survie à une faible croissance. Cependant, il y a peu d'information sur la relation entre la croissance et la mortalité pour la plupart des essences. Nous présentons trois méthodes pour estimer les fonctions de croissance et de mortalité à partir de données de terrain facilement disponibles. Toutes les méthodes utilisent le taux annuel de mortalité et le taux de croissance récent des arbres vivants et morts. Le taux annuel de mortalité est estimé à la fois par l'analyse de survie et l'approche bayésienne. Le taux de croissance est obtenu par les carottes de sondage. Les fonctions de croissance et de mortalité sont ajustées à l'aide de deux méthodes paramétriques et d'une méthode non paramétrique. Les trois méthodes sont comparées à l'aide des intervalles de confiance amorçé et des tests du rapport de vraisemblance. À titre d'exemple, les fonctions de croissance et de mortalité montrent une différence substantielle entre l'*Acer rubrum* L. et le *Cornus florida* L. dans leur capacité à survivre à une faible croissance. L'estimation du taux de mortalité par l'analyse de survie ou l'approche bayésienne conduit à des fonctions de croissance et de mortalité semblables. L'approche bayésienne permet cependant de pallier l'absence de données d'inventaire à long terme. Pour l'ajustement des fonctions de croissance et de mortalité, l'approche non paramétrique révèle que l'inflexibilité des méthodes paramétriques peut engendrer des erreurs dans l'estimation du risque de mortalité dû à une faible croissance. Ainsi, nous suggérons que les ajustements non paramétriques soient utilisés comme outil pour évaluer les modèles paramétriques.

[Traduit par la Rédaction]

Introduction

The traditional notion of "shade tolerance" classifies species according to their abilities to grow and survive under closed canopies (Burns and Honkala 1990). While research has long concentrated on growth responses at low light, attention has expanded in recent years to increasingly consider the relationship between growth and mortality (Buchman

1983; Buchman et al. 1983; Fahey et al. 1998; Kobe and Coates 1997; Kobe et al. 1995; Kobe 1996). Because growth rate integrates the effects of many variables on vigor, it serves as an index of mortality risk. Foresters have long recognized that mortality risk increases as growth rates decline (Monserud 1976). Simulation models formalize the relationship, incorporating a "growth–mortality function" that predicts the probability of mortality based on recent growth history (Botkin 1993; Pacala and Hurtt 1993; Loehle and LeBlanc 1996). Species differences in tolerance of slow growth may contribute to community composition (Pacala et al. 1996).

Unfortunately, the data needed to parameterize the relationship between growth and mortality and how it varies among species are difficult to obtain. Tree mortality is not often directly observed. Data from long-term permanent

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plots can be used both to estimate mortality rates and to fit growth–mortality functions (Buchman et al. 1983; Hamilton 1986), but such data sets are few and often include only large trees. Long or irregular sampling intervals often preclude analysis of recent growth history (Sheil and May 1996). In the absence of long-term censuses of large populations, mortality rates can be estimated from dead trees encountered in the field (Kobe et al. 1995). This method, however, requires knowledge of how long trees have been dead, and uncertain decomposition rates can make it difficult to estimate time since death. Existing methods for modeling the growth–mortality relationship are more complex than necessary. We are unaware of efforts to determine confidence levels for the mortality rates obtained by such methods and how that confidence translates to error in growth–mortality functions.

The paucity of data describing the growth–mortality relationship has led to simplistic assumptions in models that affect predictions. For example, JABOWA–FORET models assume that all species exhibit the same tolerance of low growth, resulting in predictions much different from those of models that assume species differences (Kobe 1996; Pacala et al. 1996). These conflicting predictions suggest a need for improved understanding.

In this paper, we present and test alternative methods for estimating tree mortality rates and growth–mortality functions from field data. Our analysis is presented in three parts. First, we outline functions describing mortality and its relationship to growth. Second, we present three alternative statistical models of the growth–mortality relationship. Two parametric models (A and B) entail different assumptions concerning how populations are sampled. Our method C is a nonparametric approach that shows where parametric models may fail because of inadequate data or model inflexibility.

Finally, we provide methods for estimating mortality rate, which is required by all growth–mortality models. A Bayesian approach can be used to update mortality estimates as new data accumulate. To assess how confidence in mortality rate affects confidence in growth rate as a predictor of mortality risk, we integrate the posterior density of mortality rate. We compare the Bayesian approach with survival analysis. To demonstrate and evaluate the approaches we use data that include (i) growth rates from living and recently dead *Acer rubrum* L. and *Cornus florida* L. trees, (ii) counts of living and dead stems, and (iii) sequential censuses of mortality from permanent plots. These data are part of a larger study of the growth–mortality relationship for southern Appalachian tree populations (P.H. Wyckoff and J.S. Clark, in preparation).

The relationship between growth and mortality

Growth as an indicator of risk

A growth–mortality function describes how mortality risk increases as growth rate declines. We preface our description of specific models in the next section with this section outlining elements common to all models. Let d be the event that an individual dies in a given time interval, and a be the event that it survives. The complementary probabilities of these two events are $p(d)$ and

$p(a) = 1 - p(d)$, respectively. For a data set G_N containing a sample of N trees, the likelihood that D trees die on this interval is the binomial:

$$[1a] \quad L(G_N | \beta) = \prod_{i=1}^D p(d|g_i; \beta) \times \prod_{i=1}^{N-D} [1 - p(d|g_i; \beta)]$$

where the growth–mortality function $p(d|g_i; \beta)$ is the probability of death conditioned on a risk factor (growth rate) g_i and fitted parameters β . If there is no relationship between growth and mortality (i.e., all individuals experience the same risk) then eq. 1a simplifies to the binomial

$$[1b] \quad L(G_N | \theta) = \theta^D (1 - \theta)^{N-D}$$

where the parameter θ represents the overall probability of death $p(d)$. The maximum likelihood estimate of θ is

$$[2] \quad \hat{\theta} = \frac{D}{N}$$

The probabilities in eq. 1a can be expressed in terms of an odds ratio

$$[3] \quad \frac{p(d|g)}{p(a|g)} = \frac{p(d)}{p(a)} Q$$

where

$$[4] \quad Q = \frac{p(g|d)}{p(g|a)}$$

Thus, there are three elements to model (eq. 1), including the overall probability of death $p(d) = \theta$, which is estimated as the proportion of dead trees in the sample (eq. 2) and the densities of growth rates of dead $p(g|d)$ and living $p(g|a)$ trees. These three elements fully define the mortality function, because the probability of death at a given growth rate $p(d|g)$ and its complement $p(a|g)$ are calculated from θ , $p(g|d)$, and $p(g|a)$, i.e.:

$$\frac{p(d|g)}{1 - p(d|g)} = \frac{\theta}{1 - \theta} Q$$

Equation 3 can be cast as Bayes' rule to express the probability density of deaths at growth rate g , $p(d|g, \theta)$, in terms of the overall mortality probability $p(d) = \theta$ and the density of previous growth rates for dead individuals, $p(g|d)$:

$$[5] \quad p(d|g, \theta) = \frac{p(d)p(g|d)}{p(g)}$$

where the probability density of a growth rate g is the weighted average:

$$[6] \quad p(g) = \theta p(g|d) + (1 - \theta) p(g|a)$$

The relationships in eqs. 3–6 are the basis for the models that follow.

Growth–mortality models

There are two ways to estimate the relationship between growth and mortality. The first is a direct estimate using census data. Survival analysis is appropriate here, allowing for direct analysis of how a risk indicator (e.g., growth rate) affects mortality. Unfortunately, long-term census data are rarely available. A second way to estimate growth–mortality functions sidesteps the long-term data needs by extracting mortality and growth information from trees already dead (Kobe et al. 1995). Rather than follow a population over time, this approach focuses on past-risk (represented by

growth rate). Analysis can be complex for reasons discussed below.

We derive and then compare three methods for analyzing growth and mortality. Our first method is parametric (method A), but it is not based on a binomial likelihood. We estimate growth functions $p(g|a)$ and $p(g|d)$ and mortality rate θ independently and then calculate the growth-mortality function using the odds ratio Q (eq. 3). The second method (method B), also parametric, uses a single function for growth rate and mortality, and is based on a binomial likelihood (eq. 1). These methods are compared with a third, nonparametric approach (method C).

Method A: a growth rate focus

In the absence of census data, it is still possible to estimate a growth-mortality function, provided we know mortality rate θ . The relationship can be obtained from fitted growth distributions and θ . Equation 5 can be rearranged to give the growth-mortality function:

$$[7a] \quad p(d|g, \theta) = \frac{\theta}{\theta + (1 - \theta)/Q}$$

and its complement:

$$[7b] \quad p(a|g, \theta) = \frac{1 - \theta}{1 - \theta + \theta Q}$$

where Q is a ratio of growth rates g_i of living and recently dead trees (eq. 4). We use gamma densities for growth rates, the likelihood for recently dead trees being

$$[8] \quad L(G_D | \lambda_d, \rho_d) = \prod_{i=1}^D p(g_i | d) = \prod_{i=1}^D \frac{\lambda_d^{\rho_d}}{\Gamma(\rho_d)} g_i^{\rho_d-1} \exp(-\lambda_d g_i)$$

where λ_d and ρ_d are fitted parameters. The likelihood for growth rates of live trees differs only in having parameter subscripts a rather than d and a sample size of A rather than D . In summary, this first method fits growth distributions to each data set (living and dead) separately (eq. 8) and then, together with the mortality rate, calculates the growth-mortality function using eq. 7a.

Method B: an explicit mortality focus

Method B differs from method A in that a growth-mortality function is estimated directly. Here we begin by fitting the growth-mortality relationship $p(d|g)$. We used several parametric forms, including logistic and exponential. A Weibull model fit best for most species, having likelihood:

$$[9] \quad L(G_N | \beta) = \prod_{i=1}^D p(d|g_i; \beta) \times \prod_{i=1}^{N-D} [1 - p(d|g_i; \beta)] \\ = \prod_{i=1}^D \exp \left[- \left(\frac{g_i}{b} \right)^c \right] \times \prod_{i=1}^{N-D} 1 - \exp \left[- \left(\frac{g_i}{b} \right)^c \right]$$

Unlike the growth-mortality function used in method A (eq. 7), eq. 9 does not explicitly show the mortality rate θ . However, this likelihood depends implicitly on θ , because θ represents the fraction of dead trees in the sample (eq. 2). This method provides a likelihood for the entire sample and, thus, a basis for model evaluation, but sampling considerations will often preclude straightforward application (see below).

Method C: nonparametric

Parametric models share the disadvantage that the mortality risk estimated at one growth rate depends on estimates at all other growth rates and, thus, on the distribution of data points (Lavine

1991). Problems are especially likely where data sets contain few dead trees. To evaluate our parametric estimates we compare a nonparametric model that is constrained only by the assumption that risk changes monotonically with growth rate (Ayer et al. 1955). The nonparametric model is binomial. It differs from method B in that it assumes a discrete sequence of bins θ_j that decreases monotonically with growth rate. Our algorithm begins with an arbitrarily small bin width. Growth rates of all living and dead trees are partitioned into bins $j = 1, 2, \dots, m$, and a corresponding mortality rate for each bin is determined as

$$[10] \quad \theta_j = \frac{d_j}{n_j}$$

where d_j and n_j are, respectively, the number dead and total trees in bin j . The algorithm then checks for monotonicity. Bins for which $\theta_j > \theta_{j-1}$ are expanded (increased in width), data are rebinned, and the process is continued until a monotonic sequence is achieved having likelihood:

$$[11] \quad L(N | \theta_{j=1 \dots m}, b_{j=1 \dots m}) = \prod_{j=1}^m \theta_j^{d_j} (1 - \theta_j)^{n_j - d_j}$$

where b_j is the boundary (growth rate) between bins $j - 1$ and j . Although the estimate of mortality risk in any one bin depends on adjacent bins (to achieve monotonicity), the dependency is weak relative to that of parametric models.

Relationship to a previous method

A previous method for estimating the growth-mortality function (Kobe et al. 1995) uses a likelihood function that can be written as

$$[12] \quad L(G_N | \beta) = \prod_{i=1}^D p(d|g_i; \beta_1) p(g_i | d; \beta_2) \\ \times \prod_{i=1}^{N-D} [1 - p(d|g_i; \beta_1)] p(g_i | a; \beta_2)$$

The method involves maximizing the likelihood assuming a parametric (e.g., exponential) growth-mortality function $p(d|g)$ with fitted parameter set β_1 and the growth rate densities (e.g., gamma densities) of living and dead trees ($p(g|a)$ and $p(g|d)$) with parameter set β_2 . Equation 12 embodies conflicting assumptions regarding how mortality relates to growth rate. The form of the growth-mortality function $p(d|g)$ is already defined by the choice of functional forms for growth $p(g|a)$ and $p(g|d)$ (eqs. 3-5). Imposing a new model, in the form of $p(d|g)$, amounts to adopting a new (and conflicting) assumption concerning how mortality varies with growth. Our methods A and B demonstrate how one can adopt either a growth-rate (method A) or a direct mortality (method B) function, each of which is internally consistent and less complex than eq. 12.

Mortality rate

Our three methods depend implicitly or explicitly on mortality rate θ . For a single sample, eq. 2 represents the maximum likelihood (ML) estimate of θ , but multiple censuses or large sample sizes are needed to produce acceptable confidence intervals. In practice, multiple censuses are rarely available. One alternative to direct observation involves counts of living and recently dead stems along transects (Kobe et al. 1995). To estimate θ from such data, one must determine when dead trees died. Kobe et al. (1995) judge trees to be recently dead based on twig suppleness and leaf retention. This method has the advantage of providing rapid estimates.

We found criteria for judging time since death difficult to apply and sought other means for estimating θ . The two methods we outline here use different data types and determine parameter confidence based on different criteria. Our Bayesian analysis is applied to two data types (stem counts and census data) to estimate θ and to determine how our belief in θ affects estimated mortality functions. The survival analysis that follows is an adaptation of standard methodology to tree census data, where census intervals can span multiple years or be of uneven duration.

A Bayesian estimator for mortality rate

Our Bayesian approach treats mortality risk θ as a random variable described by a probability density. The "spread" of that density reflects our knowledge of θ , which, in practice, depends primarily on sample size. We begin with a prior estimate of this density, with broad spread reflecting limited insight. Data refine our understanding, which is manifest in a posterior density concentrated about our best estimate. The analysis entails specifying a prior density for θ , which is subsequently "updated" with data. We assume a prior beta density for the parameter θ :

$$[13] \quad f(\theta) = \frac{\theta^{N_0-1}(1-\theta)^{N_0-D_0-1}}{B(N_0, N_0 - D_0)}$$

where $B()$ is the beta function, and D_0 and N_0 are prior estimates of dead and total trees, respectively. The mean for this prior is eq. 2:

$$[14] \quad E(\theta) = \frac{D_0}{N_0}$$

with variance

$$[15] \quad \text{var}(\theta) = \frac{D_0(N_0 - D_0)}{N_0^2(N_0 + 1)}$$

Additional data are used to sequentially update our density of θ . Suppose a data set yields numbers of dead and total trees D_1 and N_1 . The posterior density of θ is also a beta density:

$$[16] \quad f(\theta|D_1) = \frac{f(\theta)f(D_1|\theta)}{\int_0^1 f(\theta)f(D_1|\theta)d\theta} = \frac{\theta^{D_0+D_1-1}(1-\theta)^{N_0-D_0+N_1-D_1-1}}{B(D_0+D_1, N_0-D_0+N_1-D_1)}$$

(e.g., O'Hagan 1994). By sequential application the posterior density following m censuses is

$$[17] \quad f(\theta|D_m) = \frac{\theta^{\sum_{k=0}^m D_k - 1} (1-\theta)^{\sum_{k=0}^m (N_k - D_k) - 1}}{B\left(\sum_{k=0}^m D_k, \sum_{k=0}^m N_k - \sum_{k=0}^m D_k\right)}$$

This posterior can be integrated to obtain Bayesian confidence intervals on the growth-mortality function itself:

$$[18] \quad p(d|g, D_m) = \int_0^1 p(d|g, \theta) f(\theta|D_m) d\theta$$

where the mortality function is eq. 7a (method A) or eq. 9 (method B).

Survival analysis from sequential censuses

Survival analysis can be applied where long-term census data are available from permanent plots. Consider an initial sample of N trees at time t_0 that will be censused at successive intervals $j = 1, 2, \dots, m$. The duration of census interval j , t_j , is the elapsed time between census $j-1$ and j . D_j individuals die during interval j , and $N - \sum_{i=1}^j D_i$ remain to be tallied at the next census. Let $f(t)$ be the probability density for mortality with corresponding distribution function:

$$F(t_{j-1}, t_j) = \int_{t_{j-1}}^{t_j} f(t) dt$$

$F(t_{j-1}, t_j)$ is the probability of death during census interval j . Each individual has one of $m+1$ possible fates: it can die during one of the m census intervals, or it can survive to the end of the study. The likelihood can be written in terms of census intervals:

$$[19] \quad L(N|\theta) = \prod_{j=1}^m [F(t_{j-1}, t_j)]^{D_j} \times [F(t_m, \infty)]^{N - \sum_{j=1}^m D_j}$$

The product series incorporates the contributions of individuals that die over the successive censuses, and the survivor function incorporates those that remain alive at the last census.

Now assume a constant mortality rate θ that is continuous in the sense that mortality is not limited to a specific time during the census interval. The ML estimate of θ satisfies $\frac{\partial}{\partial \theta} \ln L = 0$, where

$$[20] \quad \ln L = \sum_{j=1}^m D_j \ln(e^{-\theta t_{j-1}} - e^{-\theta t_j}) - \left(N - \sum_{j=1}^m D_j \right) \theta t_m$$

is obtained by solving for the distribution function for constant mortality risk θ . For a single census interval of duration t we obtain a closed form solution for risk:

$$\hat{\theta} = \left[t \ln \left(1 - \frac{D}{N} \right) \right]^{-1}$$

There is no closed form solution for multiple censuses, but eq. 19 is readily solved numerically.

Combining mortality rate estimates with growth-mortality functions

Because recently dead trees are often rare, they are infrequent in stem counts and census data. Impossibly large sample sizes may be needed to obtain sufficient dead trees for confident growth-mortality fits. Whereas a modest number of dead trees may be sufficient to estimate mortality rate, large numbers are needed to estimate growth-mortality functions. For example, a mortality rate of $\theta = 0.01/\text{year}$, would require growth rates for 2000 live trees to obtain 20 from dead trees. Although 20 dead trees may yield acceptable estimates of mortality rate, this sample size may be too small for estimating the distribution of growth rates of recently dead trees (e.g., eq. 8). If we actively search for dead trees, then we lack the proportions of living and dead trees that determine mortality rate. Our sampling scheme (see Field data below) involves active search for dead trees, which provides growth rates disproportionate to their representation in the field. To fit bihomial models to such data, we describe a bootstrap procedure for weighting effects of growth data according to the estimate of their contribution to the likelihood as implied by eq. 2 (see Estimation below).

Study area

Data were obtained from the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains (35°03'N, 83°27'W). Mean annual temperature is approximately 13°C and average annual rainfall is 220 cm (Swift et al. 1988). Temperature decreases and precipitation increases with increasing elevation. Soils are primarily Ultisols and Inceptisols (Velbel 1988). Dominant overstory vegetation includes *Acer rubrum*, *Quercus prinus* L., *Quercus rubra* L., *Carya glabra* (Mill.) Sweet, and *Liriodendron tulipifera* L. Important understory species include *Cornus florida*, *Acer pennsylvanicum* L., and *Rhododendron maximum* L.

Methods

Field data

Data derive from two study areas at elevations of 800 and 1100 m. Growth rates were obtained from increment cores of living and recently dead *Acer rubrum* and *Cornus florida* trees. "Recently dead" trees were defined as standing individuals without leaves but still identifiable to species. Only dead trees with intact crowns were cored to insure that death did not result from catastrophic (and presumably growth-independent) causes.

To estimate recent growth history, we cored all recently dead trees >4 cm diameter at breast height (DBH) encountered along transects at each of the two study areas. Within approximately 10 m of each dead tree, we cored and measured diameters of conspecific live individuals of similar size. Growth increments were measured with the WINDENDRO (Régent Instruments Inc.) measuring system. We report radial growth rates averaged over the five most recent growth years. Long-term growth histories are considered in a companion paper (P.H. Wyckoff and J.S. Clark, in preparation).

To estimate mortality rates, we used three censuses from five permanent mapped plots. Plots were 40 m × 20 m when established in 1991. All trees over 2 m tall were measured in 1991, and survival was checked and the survivors remeasured in 1993. Trees were censused again in 1995. Also in 1995, the plots were expanded to 60 m × 60 m, and a recensur of the expanded plots was done in 1996.

For our Bayesian method, we used three types of prior mortality estimates. Our first prior is based on a stem count method similar to that of Kobe et al. (1995), where N_0 is the total number of individuals and D_0 is an estimate of the number that die per year. Stem counts were conducted in 5 m radius plots located at 20 m intervals along transects used for increment core sampling. Based on the characteristics of dead trees in our census plots, which died during a known interval, we estimated that trees remained identifiable to species for an average of 5 years. D_0 is therefore the total number of observed dead stems divided by five. Our second prior was taken from USDA Forest Service Forest Inventory and Analysis (FIA) plots located in the seven North Carolina counties nearest our field site (<http://www.srsfia.usfs.msstate.edu/scripts/ew.htm>). We used only FIA plots in stands of similar age and elevation as our study sites. Our third prior is taken from mortality rates of *Acer rubrum* from Missouri (Shifley and Smith 1982).

Estimation

To examine how estimates changed with accumulation of data, we estimated mortality rates incrementally, treating successive censuses as "new" data sets. Bayesian confidence intervals for mortality estimates are quantiles from the posterior density (eq. 17). Confidence intervals for survival analysis were determined by a likelihood profile (Cox and Oakes 1984).

Parameter estimates for methods A and B were determined by a nonparametric bootstrap (Efron and Tibshirani 1993). Parameter

estimates are based on 500 resamples. For method A, we first obtained ML estimates for growth densities (eq. 8) using resamples of the growth data weighted by the proportion of dead trees implied by our mortality estimates. Each resample included (i) a sample size of dead trees equal to the number of dead trees in the data set, and (ii) a sample of size of living trees of size

$$[21] \quad A' = D \frac{1 - \hat{\theta}}{\hat{\theta}}$$

where D is the number of dead trees for which growth rates have been obtained, and $\hat{\theta}$ is the posterior mortality estimate from eq. 17. For each resample, we calculated the growth-mortality function, substituting for Q in eq. 7, and we examined the effect of error in $\hat{\theta}$ on the growth-mortality function by numerically integrating eq. 18. Thus, we accommodate both sampling error in growth and confidence in the estimated mortality rate.

For method B, we used the resampling procedure to weight the contributions of living and dead trees. ML parameter estimates were obtained for each resample using eq. 9. The ML for the model is taken as the mean ML over the bootstrapped sample, because the underrepresentation of live growth rates means that there is no likelihood for a raw data set. For method C, the algorithm described by eqs. 10 and 11 was implemented on a data set having bins weighted by the proportions of living and dead trees (eq. 21). The fits of methods B and C were compared with one another and to the null model (eq. 1b) based on likelihoods taken over the same weighted sample size. The likelihoods estimated by this weighting procedure are an approximation to the likelihood that would be obtained had we sampled growth rates for all live trees.

Comparisons of the binomial models (B and C) are based on Akaike's information criterion, $AIC = 2(-\ln L + \text{number of parameters})$, where L is the likelihood of the model (eq. 9 or 11). For method B, there are two fitted parameters, b and c . For method C, the number of fitted parameters is $2m$, where m is the number of bins. The fitted parameters consist of θ_j and a boundary for each of the m bins, b_j .

Binomial models (methods B and C) were tested against the null hypothesis of no growth rate effect using the likelihood $L(G_N|\theta) \propto \theta^D(1 - \theta)^{N-D}$ and a likelihood ratio test. Method B has one degree of freedom (two fitted Weibull parameters minus one parameter for the null likelihood, θ). Method C has $2m - 1$ degrees of freedom (two for each bin minus one for the null model).

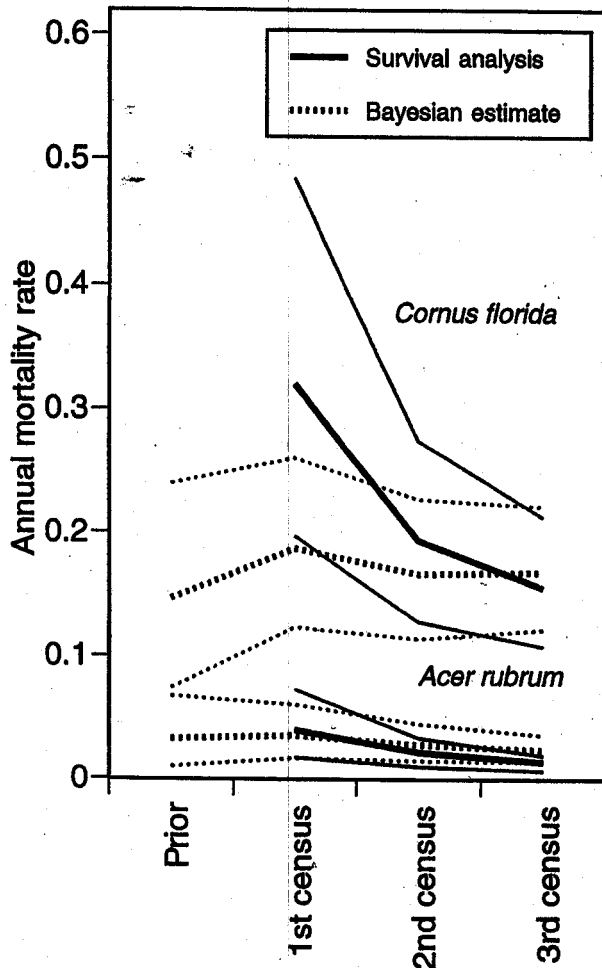
Results

We use data from *Acer rubrum* and *Cornus florida* to demonstrate our methods, because they yield contrasting mortality functions. At our study site, *Cornus florida* contracts dogwood anthracnose disease, which accounts for the poor tolerance of low growth we see in this classically "tolerant" species (Burns and Honkala 1990). Growth rates were measured for 107 living and 41 recently dead *Acer rubrum* trees and for 26 living and 28 recently dead *Cornus florida* trees.

Estimating annual mortality (θ)

Because all three methods for relating growth and mortality require an estimate of mortality rate, we begin with our estimation of θ . To determine whether Bayesian confidence intervals are strongly influenced by prior estimates, we used three priors from sources other investigators might use. Our first prior is based on stem counts. For *Acer rubrum*, our initial stem counts yielded $D_0 = 4.6$ dead (23 deaths in 5 years for an average of 4.6 dead trees/year) from a total of

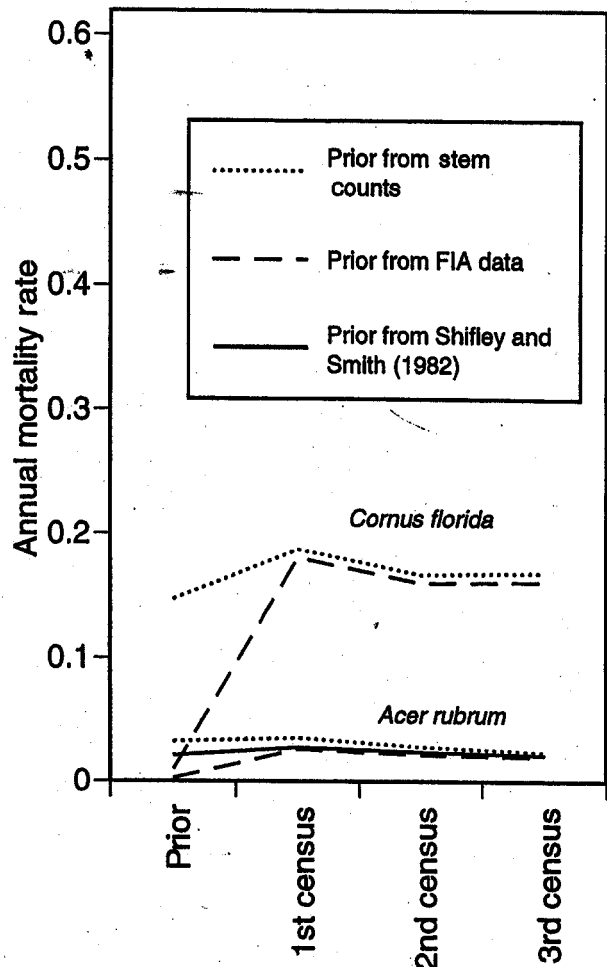
Fig. 1. Survival analysis and Bayesian estimates of the annual mortality rate θ for both *Acer rubrum* and *Cornus florida* change with the iterative addition of more field data. Note the tightening of confidence intervals (thin lines) with each iteration. The Bayesian prior is based on stem count data which are not included in the survival analysis.



$N_0 = 142$ trees. The *Acer rubrum* prior has a mean of $D_0/N_0 = 0.032$ and broad spread ($\text{var } \theta = 0.015$) (Fig. 1). Sequential application of our Bayesian method (eq. 17) using permanent plot data progressively reduces the estimated mean mortality rate to $\theta = 0.023$ ($D_0 = 17.6$ and $N_0 = 751$) and reduces the confidence interval (Fig. 1). *Cornus florida* suffers higher mortality than *Acer rubrum*. Initial stem counts yielded $D_0 = 10$ and $N_0 = 68$ for a prior Bayesian estimate of $\theta = 0.15$. The posterior Bayesian estimate of mortality is $\theta = 0.17$ ($D_0 = 36.5$ and $N_0 = 217$).

Our second prior was taken from Forest Service FIA data. In 1984, FIA plots near our field site, at similar elevations, and in forest stands of similar age, contained 68 *Acer rubrum* trees 12.7–20.3 cm in diameter. In 1990, 67 of the 68 individuals remained alive, for an average annual mortality of 0.17 trees ($D_0 = 0.17$ and $N_0 = 68$) (Fig. 2). Using our census data, the posterior estimate of mortality rate was $\theta = 0.019$, lower than that obtained using the prior based on stem counts. The FIA-based prior for *Cornus florida* included 16 trees in 1984, fifteen of which survived to 1990

Fig. 2. The effects of three alternate priors on the posterior Bayesian estimate of mortality rate for *Acer rubrum* and *Cornus florida*.



($D_0 = 0.17$ and $N_0 = 16$). Addition of census data yielded a posterior mean mortality rate of $\theta = 0.16$, slightly less than obtained using a prior based on stem counts (Fig. 2). Our third prior for *Acer rubrum* $D_0 = 4.7$ and $N_0 = 224$ comes from Shifley and Smith (1982). Addition of our census data does not change the mean mortality estimate (posterior $\theta = 0.021$).

Survival analysis of permanent plot data showed that most *Acer rubrum* mortality was confined to the initial cohort. The initial high estimate of $\theta = 0.039$ declined with the addition of the second and third cohorts to a final estimate of $\theta = 0.013$ (Fig. 1). The estimated rate for *Cornus florida* is $\theta = 0.16$ (Fig. 1).

Relating growth and mortality

Fitted growth rate densities from method A (eq. 8) show a distinction between parameter estimates (λ and ρ) for live and dead trees (Table 1), but parameter estimates are correlated (Fig. 3). Recently dead trees tend to have lower growth rates in the years just prior to death (Fig. 4). The mortality functions derived from these fits (eq. 7a) show the risk of death decreasing with increasing growth for both species;

Table 1. Parameter values for gamma (method A) and Weibull models (method B).

	Parameter	Value	95% CI
<i>Acer rubrum</i>			
Gamma model (method A)			
Living trees	λ_1	1.95	1.62–2.34
	ρ_1	1.91	1.61–2.29
Dead trees	λ_d	1.74	1.25–2.68
	ρ_d	4.42	2.40–8.55
Weibull model (method B)			
	b	0.018	
	c	0.39	
<i>Cornus florida</i>			
Gamma model (method A)			
Living trees	λ_1	4.44	2.80–7.74
	ρ_1	6.51	3.92–11.79
Dead trees	λ_d	3.28	2.17–5.81
	ρ_d	8.37	4.50–18.00
Weibull model (method B)			
	b	0.24	
	c	0.87	

this decrease is steep for *Cornus florida* (Fig. 5). Bootstrapped 95% confidence intervals show significant differences between the two species' abilities to survive radial growth rates below 0.7 mm/year.

The Weibull growth–mortality function (method B; see Table 1) and the nonparametric mortality function (method C) predict relationships similar to those obtained by method A (Fig. 6). For both *Acer rubrum* and *Cornus florida*, likelihood ratio tests of methods B and C versus the null model are highly significant (Table 2). Similar AIC values (Table 2) indicate the two methods fit the data equally well. Because Bayesian and survival analysis estimates of annual mortality for *Acer rubrum* and *Cornus florida* were nearly identical (Fig. 1), there is little difference in the growth–mortality functions predicted using either approach (Fig. 7).

Where do parametric models fail?

As an aid to visualizing the level of agreement between models and data, we used a kernel smoother to estimate nonparametric densities for $p(g|d)$ and $p(g|a)$ (Silverman 1986; function “density” in SPLUS). The joint density $p(g,d)$ is the product $p(g|d)p(d)$. The nonparametric conditional densities are then

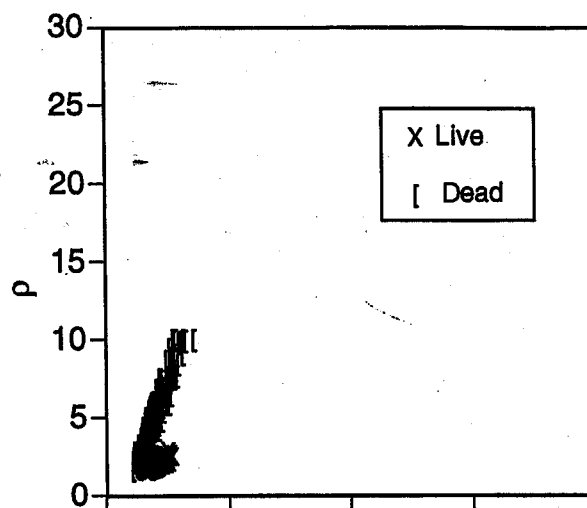
$$p(d|g) = \frac{p(g,d)}{p(g)}$$

The resulting smoothed data are compared with the Weibull function (method B) in Fig. 8. Unlike our method C, the smoothed kernel need not be monotonic.

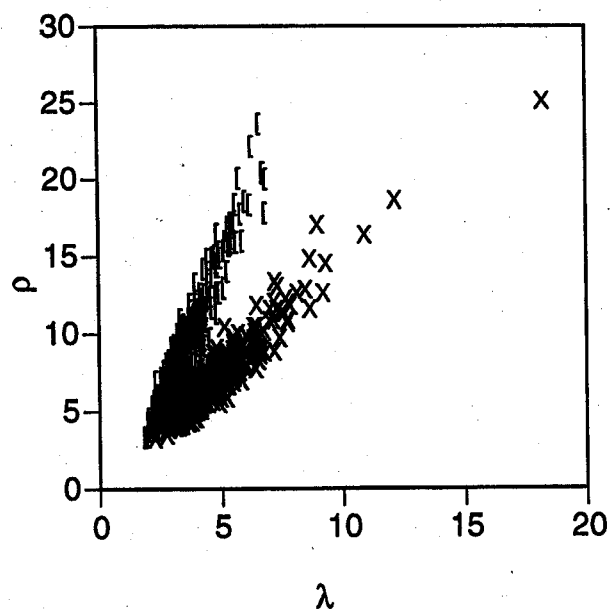
The nonparametric method C and the smoothed data indicate that the parametric models (A and B) fail to capture the

Fig. 3. Gamma parameters λ and ρ (eq. 8) from each of 500 bootstraps for the growth rate distributions of (a) living and recently dead *Acer rubrum* show differences in parameter ρ . For (b) living and recently dead *Cornus florida*, parameter values show broad overlap.

(a) *Acer rubrum*



(b) *Cornus florida*

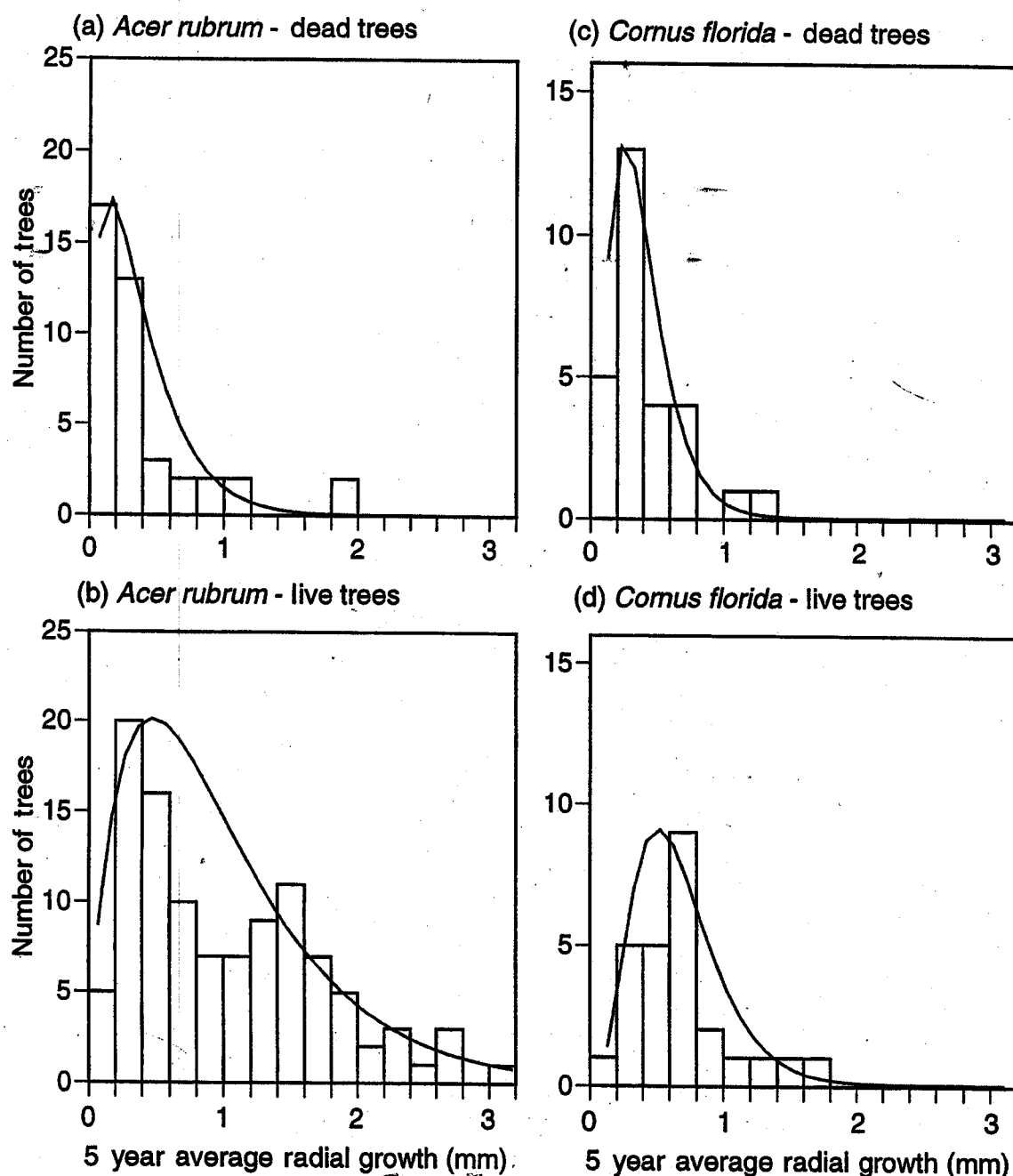


steepness of the increase in mortality risk that occurs at low growth rates (Figs. 6 and 8). Figure 9 shows this low-growth region for *Acer rubrum*. The parametric models are inflexible and do not reflect the abrupt increase in risk below 0.1 mm annual radial growth.

Discussion

A growth–mortality function is an empirical summary of the complex relationship involving environmental stress, growth, and mortality risk. Slow growth indicates low vigor

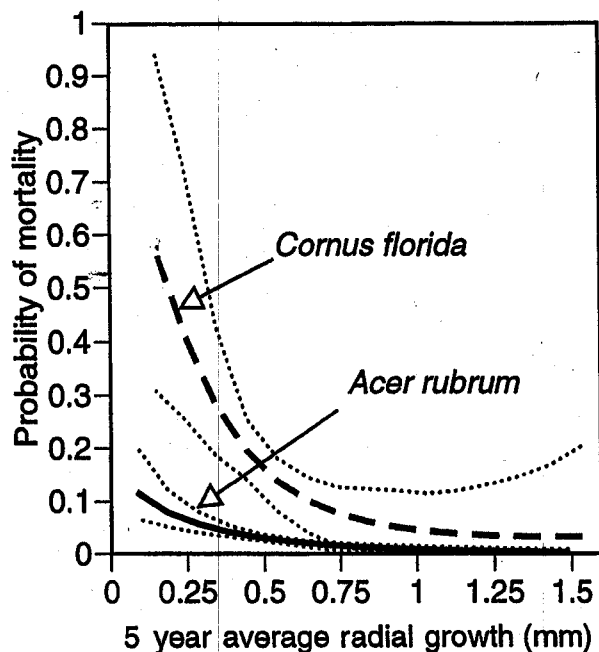
Fig. 4. Growth rate distributions (histograms) of (a) recently dead and (b) living *Acer rubrum* and (c) recently dead and (d) living *Cornus florida* with their respective gamma fits (solid lines). Note that living trees grew faster than recently dead trees for both species.



and risk from a variety of agents. The value of these empirical relationships is evident from a long tradition of their use in simulation models (Botkin et al. 1972; Shugart and West 1977; Huston and Smith 1987) and from the more direct evidence they provide concerning successional status (Kobe et al. 1995; Pacala et al. 1996). Because of their implications for the overall dynamics of forest communities, the availability of confident estimates extends insight into how life history affects succession and diversity. The difficulty obtaining such estimates is reflected in the simplistic (e.g., step) functions traditionally used in such models

(Botkin 1993) and development of creative new field methods (Kobe et al. 1995). We contribute modeling approaches that permit estimates under the sampling constraints that are typical for such data. Our three methods for analyzing the relationship between growth and mortality derive from different statistical models, but they give similar results (Fig. 6). Each method has its advantages, and there are important differences. Before discussing the relative merits of our three approaches, we evaluate our ability to estimate mortality rate, θ , because each of our three methods depend on it.

Fig. 5. Fitted mortality functions for *Acer rubrum* and *Cornus florida* based on method A. Broken lines are bootstrapped 95% confidence intervals.



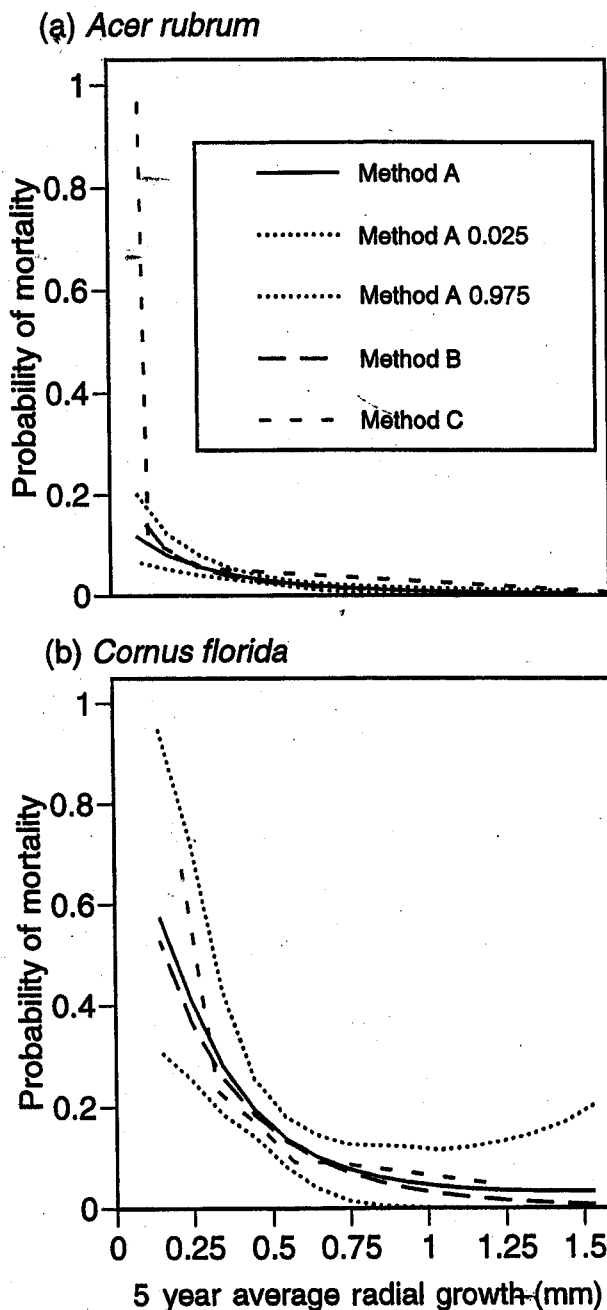
How well can we estimate mortality rate?

Although there are many published studies of tree mortality, model comparison is rare, and statistical inference tends to be neglected (Clark et al. 1999). For the case where mortality can occur at any time during a census interval (it is not discrete), survival analysis (based on eq. 20) offers a less biased estimate of θ than does the traditional method of using the fraction of trees that die divided by the duration of the interval. Survival analysis with our census data provide confident estimates (Fig. 1).

The Bayesian approach is valuable when data are limited, because it exploits prior information that can be extracted from other sources, and it explicitly accommodates parameter variability. Strength of our prior estimate of θ is determined by sample size. Because the amounts of data contributing to our first two priors, one based on stem counts and one based on FIA data, were small relative to our censuses, alternative priors did not have large effects on final estimates (Fig. 2). Had these prior estimates been based on larger samples, the effect on the posterior would have been more noticeable. A third prior obtained from the literature (Shifley and Smith 1982), was based on a large sample. Because this prior was similar to our census data, it sharpened the posterior without affecting the mean.

Caution may sometimes be needed in choosing appropriate priors. The USDA Forest Service FIA data only include stems >12.5 cm DBH, thus excluding the small individuals that tend to suffer highest mortality rates. In the case of *Cornus florida*, the FIA data derive from the period before dogwood anthracnose entered the area, so mortality rates were low (see Fig. 2, prior from FIA data). Standard methods can be used to test for Bayesian robustness, i.e., sensitivity to the prior (Gelman et al. 1995).

Fig. 6. Mortality functions based on parametric methods A and B and the nonparametric method C for (a) *Acer rubrum* and (b) *Cornus florida*. Broken lines are bootstrapped 95% confidence intervals for method A.



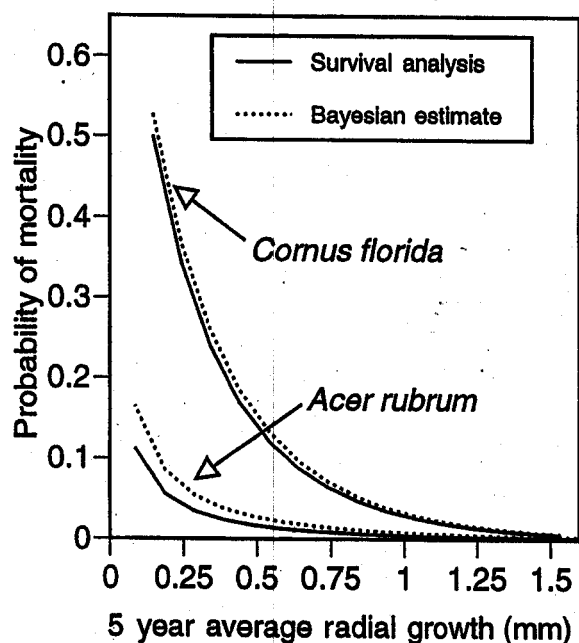
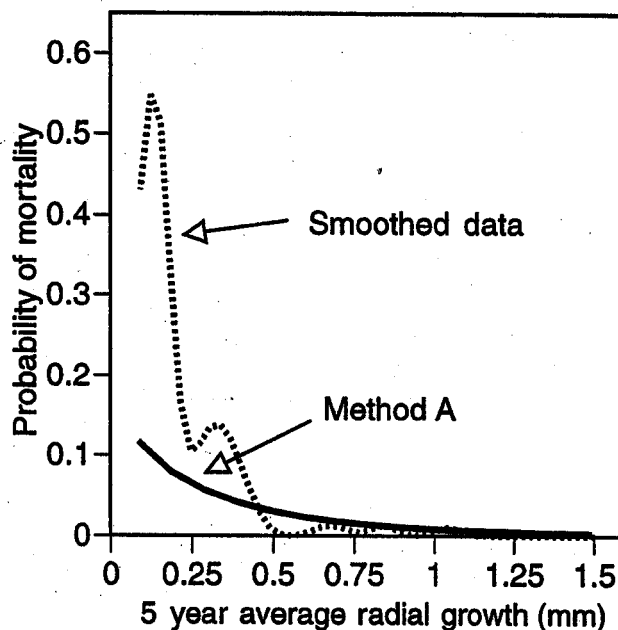
The beta posterior that we obtain from our conjugate beta binomial prior is especially valuable for error propagation. It represents a parametric function that can be inserted in eq. 18 and used to produce the confidence intervals on the growth-mortality function itself (Fig. 5).

Which growth-mortality model?

Estimating growth-mortality functions is frustrated by the relative rarity of dead trees. In the case where full sampling is possible (when the growth rates of live and dead trees are

Table 2. Model comparisons.

Model	Negative log likelihood	<i>p</i> value of likelihood ratio test vs. null model	No. of parameters	AIC
<i>Acer rubrum</i>				
Null	194.4	—	1	391.0
Method B	168.0	<0.0001	2	340.0
Method C	162.7	<0.0001	8	343.3
<i>Cornus florida</i>				
Null	78.5	—	1	158.9
Method B	64.5	<0.0001	2	133.1
Method C	63.3	<0.0001	8	142.6

Fig. 7. Method B survival functions based on both survival analysis and Bayesian estimates of annual mortality rate θ .Fig. 8. Deviation between smoothed data and parametric method A for *Acer rubrum* shows that method A fails to capture the sharp increase in mortality risk seen at low growth rates.

sampled in proportion to their natural abundances), method B provides the most direct estimate of the growth–mortality relationship. Large and long-term data sets (e.g., Condit et al. 1993a, 1993b) are best suited for analysis by method B. In the case where growth rates cannot be sampled in proportion to their relative abundances, mortality rate might be estimated from other information and used to calculate the growth–mortality relationship by method A.

Because all three models give similar predictions (Figs. 6a and 6b), we expect that parametric methods (A and B) will perform equally well for data sets comparable in size with those analyzed here. In the *Acer rubrum* example, the Weibull mortality function (method B) more closely matches the nonparametric fit in low growth regions than does our method A (Fig. 6a), but for *Cornus florida*, the opposite is true (Fig. 6b).

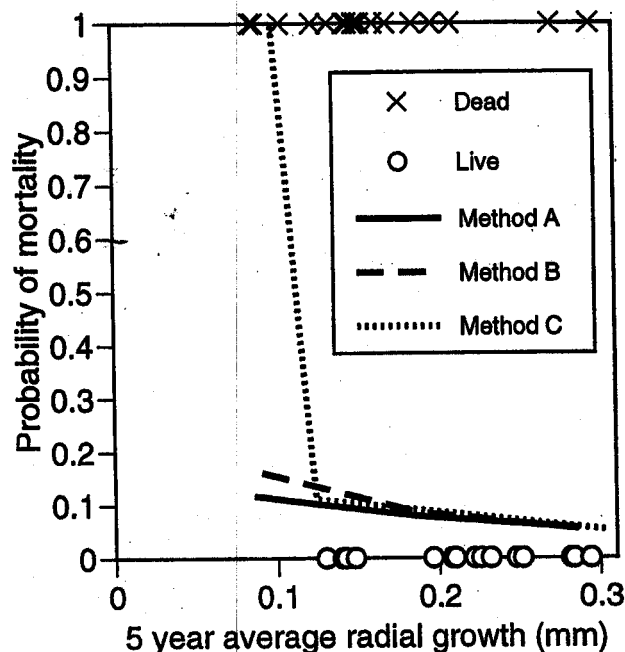
Although the nonparametric approach is least likely to be biased by the distribution of data, it is best used as a means for evaluating parametric fits, rather than as a replacement for them. Our analysis indicates parametric models are least

accurate at the lowest growth rates (Fig. 6a). The nonparametric method helps identify the problem and may suggest alternative parametric forms. Nonetheless, parametric models are needed for forest simulation models, and they are more analyzable than are nonparametric models.

Implications for forest models

Gap-dynamic forest simulation models have traditionally included the assumption that all species exhibit the same tolerance of low growth. JABOWA–FORET models assume that trees only experience growth-related mortality when radial growth rate falls below 0.5 mm/year (Fig. 10). Our mortality functions show mortality risk at higher growth rates. Preliminary results show that incorporation of our mortality functions into the LINKAGES gap-dynamic model (Pastor and Post 1985) substantially alters that model's predictions of successional dynamics of southern Appalachian forests (P.H. Wyckoff and J.S. Clark, in preparation). Pacala et al. (1996) also found that growth–mortality functions calculated

Fig. 9. Deviation between parametric methods A and B and nonparametric method C mortality functions for *Acer rubrum* at very low growth rates. Actual data points are shown as O (for recently dead) and X (for live trees).



by Kobe et al. (1995) affect predictions of forest succession. Continued improvement in forest simulation models requires more data. The methods described here provide a basis for analysis and inference.

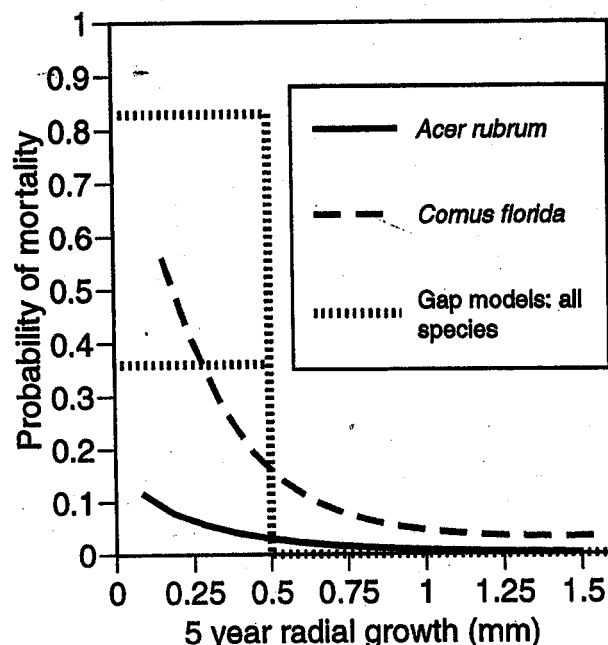
Conclusions

Our three approaches provide tools for estimating the growth–mortality relationship for tree species in the absence of large, long-term data sets. Our Bayesian approach accommodates prior mortality information and yields a parametric posterior. We propagate error in estimates of mortality rate and assess the effect on the confidence in the growth–mortality function. Our nonparametric method C provides a tool to assess the performance of parametric approaches in capturing the vital low growth – high mortality regions of the growth–mortality curve. Accurate simulation of forest dynamics depends on the field estimates of mortality risk that these methods can provide.

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Fig. 10. Mortality function from JABOWA–FORET models compared with method A mortality functions for *Acer rubrum* and *Cornus florida*. In JABOWA–FORET models, all species experience the same slow-growth mortality risk. Two consecutive years of radial growth below 0.5 mm leads to a 37% mortality risk. After five consecutive years of growth below 0.5 mm, trees experience an 84% mortality risk. There is no risk of growth-related mortality at growth rates above 0.5 mm, and one good year of growth resets the mortality risk to zero no matter how long a tree has been suffering from poor growth.



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